Plant Physiol. (1998) 116: 1–7

Update on Plant-Plant Communication

Plant-Plant Communications: Rhizosphere Signaling between Parasitic Angiosperms and Their Hosts[1]

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Plants are in constant communication with a multitude of diverse organisms. Some symbioses, such as the association of nitrogen-fixing bacteria and mycorrhizal fungi with plant roots, are beneficial to the plant. Others, such as the interaction of plants with viral, microbial, fungal, and nematode pathogens, are harmful. Most plant-organism interactions go unnoticed simply because they are underground. A single gram of fertile soil can contain 10^9 bacteria, 10^6 actinomycetes, and 10^5 fungi, as well as several millimeters of roots. Populations in the rhizosphere, the narrow zone of soil surrounding a root, may be 1 or 2 orders of magnitude higher.

Plants are not passive targets for associating organisms but, rather, actively affect the structure of rhizosphere communities by releasing attractants and repellents from their roots. As much as 20% of a plant's net photosynthate is released into the rhizosphere. Large quantities of phenolic compounds are also released from plant roots; approximately 120 kg/ha plant-derived phenolics can be added into grassland soil annually. Many of these strongly affect neighboring plant and microbial communities (Siqueira et al., 1991). Other signals released from plant roots are more subtle and are specifically directed toward attracting or repelling particular colonizers. An important conclusion from several recent studies is that interactions between plants and other organisms are mediated by signal molecules that cue developmental and physiological events critical in the interaction (Baker et al., 1997).

In natural environments plants are intimately associated with other plants. Epiphytes such as orchids, bromeliads, and Spanish moss grow on other plants, using them for support. Plants such as Indian pipe (*Monotropa uniflora*) indirectly obtain nutrients from other plants via mycorrhizal bridges that connect them with host roots. A more direct plant-plant interaction is between parasitic plants and their hosts (Press and Graves, 1995). Parasitian originated at least eight times independently in the evolution of higher plants and about 3000 species of angiosperms (approximately 1%) are parasites (Kuijt, 1969; Parker and Riches, 1993). Parasitic plants have different modes of invading host plants; some invade host root, whereas others invade aerial parts of the plant. In all cases invasion of host tissues and extraction of host resources is mediated by haustoria, specialized multifunctional organs that uniquely define parasitic plants. In this review we will discuss how haustorium development in root-parasitic plants is cued by host plant signals.

Several parasitic plants are significant agricultural pests. For example, dwarf mistletoes (*Arceuthobium* spp.) are responsible for the annual loss of more than 3.2 billion board feet of lumber in the United States because of reduced and deformed growth of infected conifers (Parker and Riches, 1993). However, the parasitic plants with the greatest impact worldwide are the root parasites in the Scrophulariaceae and closely related Orobanchaceae families. Crops susceptible to these parasites include important cereals such as maize, sorghum, millet, and rice, as well as legumes and other vegetables. *Striga* spp. are particularly notorious, infecting more than two-thirds of the 73 million ha of cereals and legumes in Africa. Yield losses by infection with these parasites often reach 100%, and levels of infestation are frequently so great that continued crop production becomes impossible. The Food and Agriculture Organization of the United Nations estimates that the lives of more than 100 million Africans in 25 countries are threatened by crop losses due to *Striga* spp. Because of their significance to agriculture, most parasitic plant research, and consequently most of this review, concerns plants of the parasitic genera Scrophulariaceae.

HOST RANGE AND SPECIFICITY

The degree to which a parasitic plant is dependent on host resources varies tremendously. At one extreme are holoparasites such as *Orobanche* spp., which lack chlorophyll and therefore rely on host photosynthate and other nutrients for survival. Members of the *Striga* genus are photosynthetically competent and are therefore termed hemiparasites. Nonetheless, *Striga* spp. are obligate parasites, since they must attach to a suitable host soon after germination to survive. Many parasitic Scrophulariaceae species, including those of the genera *Pedicularis*, *Rhinanthus*, *Agalinis*, and *Triphysaria*, are facultative parasites that can reach maturity without parasitizing a host. In natural

[1] This work was supported in part by National Science Foundation grant no. 94-07737 and by the Rockefeller Foundation.

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Abbreviations: CPBQ, cyclopropyl-*p*-benzoquinone; DMBQ, 2,6-dimethoxy-*p*-benzoquinone; HIF, haustoria-inducing factor.

settings, however, facultative parasites are almost always associated with host plants. For many reasons, obligate parasites are considered more evolutionarily advanced than facultative and nonparasitic plants (Kuijt, 1969). All of the evolutionarily stages of parasitism are represented in a single, monophyletic clade of the Scrophulariaceae (dePamphilis et al., 1997).

The number of potential hosts that can be infected by any particular parasitic species is also varied (Parker and Riches, 1993). The term host specificity is reserved for extreme cases when host preference is narrowly restricted. Obligate parasites generally have more specific host requirements than facultative parasites. The host range of dwarf mistletoes is generally restricted to the genus *Pinus* and occasionally to a single species within *Pinus*. The genus *Striga* consists of 35 species, some of which parasitize monocots and others infect dicots. For example, *Striga hermonthica* infects only monocots, including maize, sorghum, millet, rice, and sugarcane, whereas *Striga gesneroides* infects only dicots. Within *S. gesneroides* are races that are specific for growth on indigo (*Indigofera* spp.), cowpea (*Vigna sinensis*), tobacco (*Nicotiana tabacum*), and *Jacuemontia* spp. (Musselman and Parker, 1981). Similarly, although the host range of Orobanchaceae is very broad, *Orobanche cernua* is restricted to sunflower and a few Solanaceae, particularly tomato, tobacco, and eggplant (Parker and Riches, 1993).

The parasitic plants with the largest host range tend to be facultative parasites. As examples, the host range of the genus *Pedicularis* includes 80 species in 35 monocot and dicot families and that of the genus *Rhinanthus* includes at least 50 species in 18 families (Gibson and Watkinson, 1989). Under experimental conditions, many facultative root parasites seem to parasitize any plant species with which they are presented.

The range of potential hosts is, however, different from the range of preferred hosts. In field studies with *Aureolaria pedicularia*, almost 99% of the haustoria observed were attached to oak (Fagaceae) roots, even though these represented less than 40% of the total roots available, demonstrating that parasitic plants can selectively parasitize the roots of favored hosts (Werth and Riopel, 1979). Also, associations with some hosts are more beneficial to the parasite than others. The growth of plants in the genera *Rhinanthus*, *Euphrasia*, *Orthocarpus*, and *Alectra* are all significantly stimulated when attached to leguminous hosts as opposed to nonlegumes. For example, *Rhinanthus minor* plants grown with *Trifolium* spp. were 10 times bigger than those grown with the nonlegume *Echium* spp. (Seel et al., 1993). The size difference was reflected in photosynthetic rates 5 times higher in the parasite after attachment with legumes.

Atsatt and Strong (1970) measured the fecundity of individual *Castilleja exserta* plants growing on six different hosts. On the average, growth on *Spergula arvenis* (Caryophyllaceae) and *Hypochoeris glabra* (Compositeae) significantly exceeded that on *Festuca myuros* (Poaceae) or *Trifolium* spp. (Leguminaceae). Growth responses varied significantly between different individuals of the same *Castilleja* spp. on the same host. For all hosts, at least some *Castilleja* spp. individuals did not derive any apparent benefits. This means that different members of a single outbreeding population preferentially parasitize different hosts. These authors suggest that this is an important evolutionary characteristic of parasitic species living in annual grassland communities, where dominant species change from year to year.

Some host associations are likely disadvantageous to the parasite and should be avoided. An interesting example of this is self-parasitism. Many workers have reported the low frequency with which haustoria form between different roots of the same plant, an association with little conceivable advantage to the parasite. We have shown that conspecific associations (between individuals of the same species) are similarly unfavorable (Yoder, 1997). *Triphysaria* is a broad host range parasite that readily parasitizes Arabidopsis. When single *Triphysaria versicolor* seedlings were grown with Arabidopsis, more than 90% formed haustorial connections. In comparison, less than 5% of the *T. versicolor* formed haustoria when grown either without a host or in the presence of a second *T. versicolor*. When a different *Triphysaria* species, *Triphysaria erianthus*, was grown with *T. versicolor* under the same conditions, about 25% of the *T. versicolor* formed haustorial connections. Apparently, there are subpopulations of *T. versicolor* that recognize congeneric but not conspecific individuals as potential hosts.

The ability of *Triphysaria* to distinguish their own roots from those of other plants is an uncharacterized form of self-recognition. In many plant-microbe symbioses, specificity is governed by the exchange and recognition of molecular signals between partners. Whether similar mechanisms control self-recognition, host preference, and host specificity in parasitic plants is largely unknown. For the remainder of this review we will examine some of the signals that are exchanged between parasitic plants and their hosts with a particular focus on those that might mediate host selectivity. An overview of the different signal pathways utilized by parasitic plants is shown in Figure 1.

SIGNAL EXCHANGE

Germination

Seeds of most parasitic plants will readily germinate if the appropriate environmental conditions with respect to water, oxygen, temperature, and light are met. However, some parasites such as those of the genera *Striga*, *Alectra*, and *Orobanche*, rely on host-derived germination factors. The identification of germination stimulants has been an area of active investigation and has been reviewed extensively (Boone et al., 1995). The first *Striga* germination factor isolated from a natural host was SXSg (Fig. 2, no. 1; Fate and Lynn, 1996). SXSg is a dihydroquinone that is quickly auto-oxidized into the inactive quinone sorgoleone. The biosynthetically related compound resorcinol (Fig. 2, no. 2) retards the auto-oxidation of SXSg, thereby reducing the effective concentration of SXSg needed for germination of *Striga* seeds.

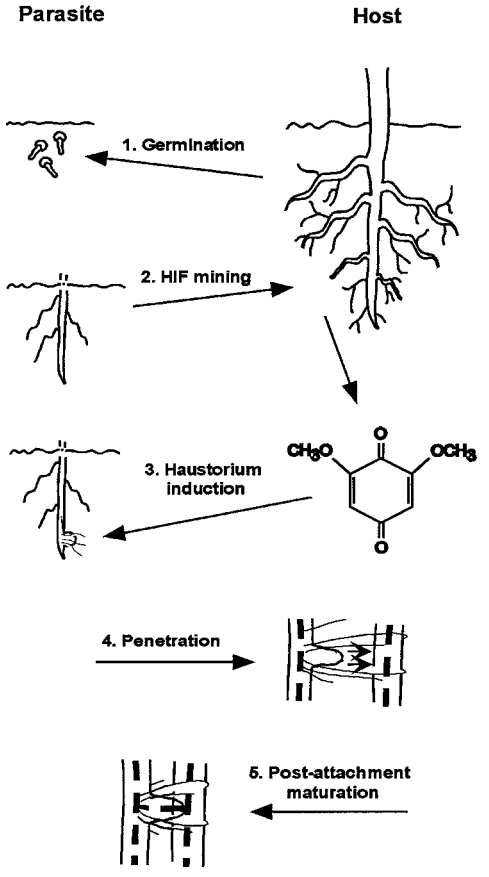

Figure 1. Molecular signals exchanged between parasitic plant and host. Five developmental stages in plant parasitism are shown. The details of each stage are discussed in the text. HIF mining refers to the parasite-controlled, enzymatic extraction of HIFs from host roots. In steps 4 and 5, haustorial hairs are shown grasping the host root, and xylem elements are represented by dashed lines. The arrows indicate the direction of signal movement between the parasitic plant on the left and the host plant on the right.

For parasites dependent on germination factors, host specificity is determined in large part by the ability of the host to produce a germination stimulant. For example, the differential growth of *S. hermonthica* races on sorghum and millet is due to variation in the production of germination stimulants (Parker and Riches, 1993). However, this is not the complete story, since several nonhost plants produce germination stimulants. Indeed, the first germination signal identified, strigol, was isolated from the roots of cotton, a nonhost.

Haustorium Induction and Preattachment Development

The haustorium is a multifunctional organ that attaches to the host, establishes a xylem continuum, and directs the unidirectional flow of nutrients into the parasite. Morphologically, haustoria appear as swollen, rounded structures attached to a host surface. In the Scrophulariaceae, haustoria develop from changes in the growth and development of specific cells in the root in response to external stimuli.

The observation that parasitic plants require the presence of host plants to form haustoria suggested that host factors could induce haustoria development. The first host-derived HIFs, xenognosin A (Fig. 2, no. 3) and xenognosin B (Fig. 2, no. 4), were isolated from foliar extracts of *Astragalus gummifer* (Lynn et al., 1981). Subsequently, DMBQ (Fig. 2, no. 7) was isolated from sorghum roots extracted with a mixture of dichloromethane and methanol (Chang and Lynn, 1986). In fact, many structurally related phenolics have been identified as HIFs (MacQueen, 1984; Smith et al., 1996).

The responses of parasite roots to HIFs are rapid and, with minor variations, similar among different parasitic Scrophulariaceae (Baird and Riopel, 1983). Within hours after applying HIFs to the parasite roots, radial expansion and, to a lesser extent, cellular division occurred in cortical cells near the root tip (Fig. 3a). At about the same time there was a proliferation of epidermal hairs localized over the swollen region. Within 24 h of treatment with HIF, the swollen, hairy, preattached haustoria were then easily visualized (Fig. 3b). The haustorium was then competent to attach to the host root.

Compounds that induce haustorium formation can be classified into four groups: flavonoids, *p*-hydroxy acids,

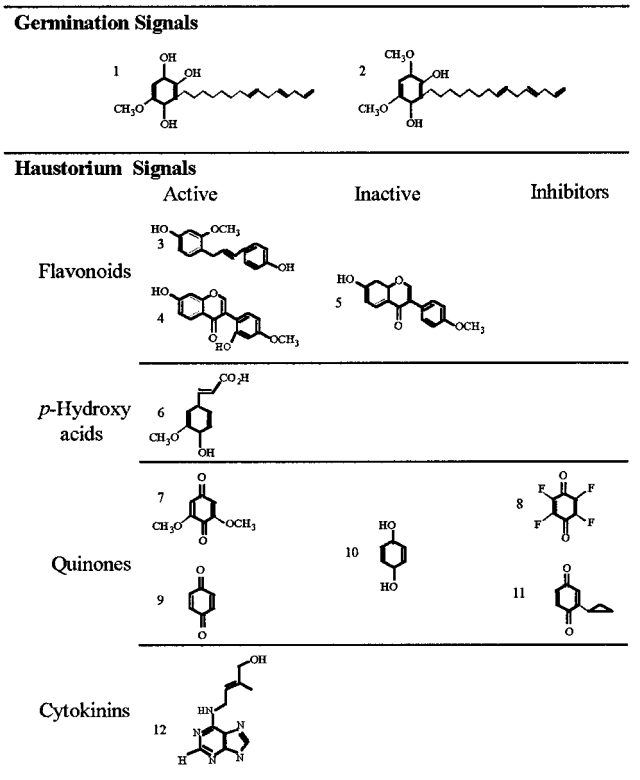

Figure 2. Signals involved in plant-parasite interactions. Examples of both germination and haustorium signals are drawn. Active compounds induce haustorium development, whereas inactive compounds do not induce haustorium development. Inhibitors reduce the HIF activity of DMBQ. 1, SXSg; 2, resorcinol; 3, xenognosin A; 4, xenognosin B; 5, formononetin; 6, ferulic acid; 7, DMBQ; 8, tetrafluorobenzoquinone; 9, benzoquinone; 10, dihydroquinone; 11, CPBQ; and 12, zeatin.

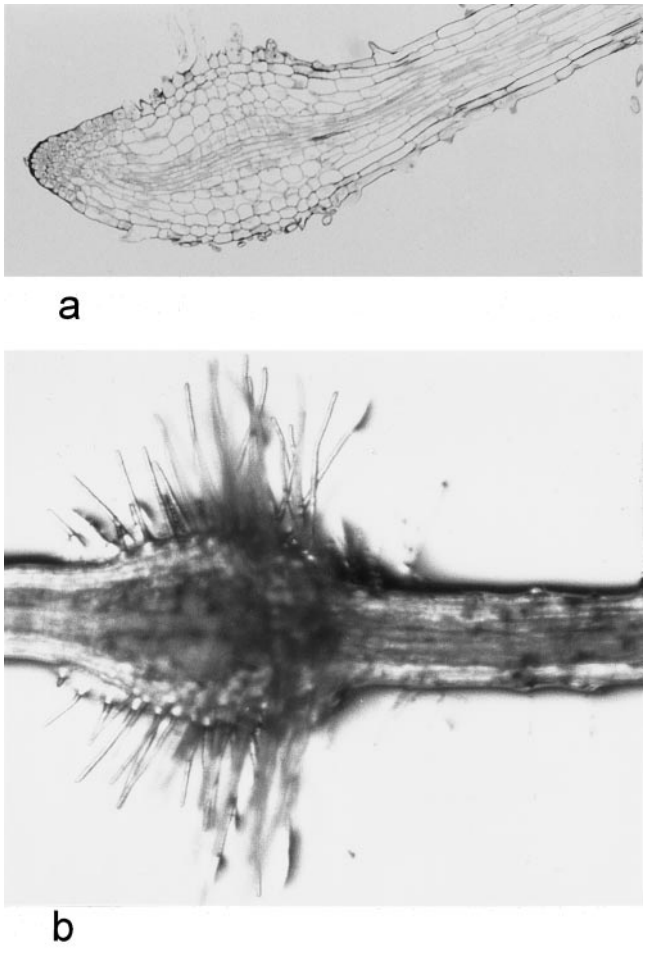

Figure 3. Preattached haustoria induced in the roots of *T. versicolor*. a, *T. versicolor* roots induced with HIFs from Arabidopsis root exudate. Forty-eight hours after induction, the roots were fixed in FAA (10% formaldehyde, 5% acetic acid, 40% ethyl alcohol), longitudinally sectioned, and observed under light microscopy. The section shows the radial expansion of cortical cells and some cell division. b, *T. versicolor* roots were treated with 10 μM DMBQ. The developing haustorium was photographed 24 h later under a dissecting light microscope without fixation. The swelling and localized hair proliferation are typical of preattached haustoria.

quinones, and cytokinins (Fig. 2; Lynn and Chang, 1990). The first three groups are structurally related phenolics derived from the common biosynthetic intermediate Phe. Smith et al. (1996) suggested that these molecules induce haustoria by a common redox mechanism, which is discussed below. Cytokinins, for example zeatin (Fig. 2, no. 12), are structurally distinct from the phenolic HIFs and presumably do not directly interact with host phenolic receptors. Cytokinins, or rather the ratio of cytokinins to auxins, are also able to induce root nodule formation in legumes (Heidstra and Bisseling, 1996). This suggests that at some stage the signals leading to haustoria and nodules converge through the manipulation of growth regulators.

Structural analyses of phenolic HIFs have not been completely adequate for understanding the structural requirements for active inducers (Steffens et al., 1982). Early studies with analogs related to the xenognosins (Fig. 2, nos. 3 and 4) first pointed toward the importance of the *m*-methoxyphenol and propene groups. However, formononetin (Fig. 2, no. 5), which is structurally similar to xenognosins but lacks the *m*-methoxyphenol group, has no inducing activity. Later, *p*-hydroxy acid HIFs, for example, ferulic acid (Fig. 2, no. 6), showed that *m*-methoxyphenol groups were not required for activity (MacQueen, 1984). The identification of DMBQ (Fig. 2, no. 7) as a haustorial inducer pointed toward the importance of a methoxyketone group (Chang and Lynn, 1986). However, the recent report that benzoquinone (Fig. 2, no. 9) is 4 orders of magnitude more active than DMBQ indicates that these substitutions are not required but, rather, are tolerated (Smith et al., 1996). Some substitutions, such as alkyl and dialkyl structures, render the quinones inactive. Nevertheless, the lack of common structural motifs among phenolic HIFs suggests that factors other than steric considerations are important.

An important observation for understanding how phenolic HIFs may interact with a parasite receptor was that the inducing activity of different quinones is correlated with their redox potential (Smith et al., 1996). The redox potentials of biologically active quinones are within a range of about 300 mV, and molecules that fall outside of this window are largely inactive. This suggests that HIFs initiate haustoria development through a redox mechanism, i.e. the transfer of electrons controlling the activity of proteins or other molecules. The contrasting activity of several redox pairs, for example, benzoquinone (Fig. 2, no. 9) and dihydroquinone (Fig. 2, no. 10), suggests that the reduced product is itself not active and but rather that the reduction process drives haustoria induction.

Inhibitors of DMBQ further elucidate the importance of a reduction reaction for haustoria induction (Smith et al., 1996). Tetrafluorbenzoquinone (Fig. 2, no. 8) is easily reduced to the hydroquinone within the narrow redox potential identified for inducers but is a reversible inhibitor of DMBQ. Smith et al. (1996) postulated that this is because tetrafluorbenzoquinone is not easily reoxidized within the redox potential range of inducers and that the semiquinone intermediate is important for induction. Additional support that the reduction process initiates haustorium development is provided by CPBQ (Fig. 2, no. 11), an irreversible inhibitor of DMBQ. The reduced form of CPBQ does not inhibit DMBQ, which is consistent with the lack of activity demonstrated by reduced quinones. What is unique about CPBQ is that, upon generation of the semiquinone, the cyclopropane substituent of CPBQ can undergo rearrangement. These rearrangements are hypothesized to block further reduction by the receptor of HIFs.

Of possible significance to haustorium induction by a redox reaction is the effect of partially active compounds. Two molecules, syringaldehyde and hydroxybenzoic acid, partially induce haustoria through only radial expansion and swelling of the root tip; there is no hair formation or further development (Riopel and Timko, 1995). The same partial development of haustoria is mimicked by DMBQ exposure times of less than 6 h (Smith et al., 1990). Partial haustorium development might reflect insufficient reduc-

tion of the partially active HIFs or insufficient oxidation of the electron donor.

One mechanism used by both prokaryotes and eukaryotes to regulate gene expression in response to different environmental cues involves transplasma membrane redox control. Proteins and processes thought to be controlled by redox reactions include transcription factors, hormone receptors, light-regulated processes, translational regulation, and defense responses. For example, redox control regulates the *Escherichia coli* transcriptional activator OxyR (Storz et al., 1990). The mechanism governing OxyR activation is mediated by the oxidation state of the protein. Irrespective of the oxidation state, OxyR binds DNA but in the reduced state is transcriptionally inactive. Oxidation of OxyR results in a conformational change that allows transcription of peroxide-inducible genes encoding proteins responsible for the degradation of reactive oxygen species.

Parasite Probing for HIFs

Phenolics make up a significant component of plant cell walls and are used for several functions, including lignin biosynthesis, pathogen defense, and symbiont signaling. *p*-Hydroxy acids and flavonoids are prevalent in roots and are commonly found in root exudates (Siqueira et al., 1991). However, attempts to isolate HIFs from root exudates of undisturbed roots have been unsuccessful. For example, exudates of sorghum roots grown with minimal agitation have no induction capacity, and yet activity is recovered when the roots are mildly abraded (Lynn and Chang, 1990). Chang and Lynn (1986) hypothesized that ligninolytic peroxidases produced by the parasite extract phenolic molecules from the host cell walls and convert these to the appropriate quinone forms. Substantial precedent exists for such enzymes in fungal and bacterial systems, and increasingly so for plants. The fungus *Phanerochaete chrysosporium* degrades the phenylpropanoid polymer lignin to its component alcohols using four classes of extracellular enzymes: lignin peroxidases, manganese peroxidases, glyoxal oxidases, and laccases (Cullen, 1997). HIFs such as benzoquinone and DMBQ are common products of these reactions. Laccases, peroxidases, and hydroxylases also oxidize *p*-hydroxy acids to quinones (Lynn and Chang, 1990). Similarly, flavonoids are also degraded into phenolic acids by different fungi and bacteria, the end products being defined by the class of degrading organisms as well as the initial substrate (Siqueira et al., 1991).

The presence of oxidative enzymes capable of generating quinones has been demonstrated in the roots of parasitic plants. Histochemical staining of *Agalinis* and *Striga* identified the presence of oxidative enzymes on the root tips (Chang and Lynn, 1986). Furthermore, when Lynn and Chang (1990) added either syringic acid or host-surface material to *Striga* cultures, DMBQ was detected by HPLC prior to haustoria development. DMBQ was not present in the host surface material prior to its addition to *Striga* DMBQ was also not detected if the *Striga* roots were washed prior to the addition of syringic acid or host root materials. Together, the evidence supports the model that parasite enzymes are released into the rhizosphere, where they probe the environment for host root signals.

Penetration

Attachment of the parasite to the host is facilitated by mucilaginous substances produced by haustorial hairs (Baird and Riopel, 1983). Attachment is not discriminatory and can occur on plastic or string as readily as host roots.

The incomplete penetration of haustoria into nonhost roots suggests that host specificity might be related to the breakdown and entry of the parasite. Penetration is mediated by a combination of intrusive growth and enzymatic digestion (Kuijt, 1969). The evidence for intrusive, mechanical penetration comes from the appearance of crushed host cells at the site of haustoria entry. Precedence for mechanical invasion of host tissues comes from fungi. The appressorium of the rice blast fungus *Magnaporthe grisea* has reduced melanin levels at the site of contact with the host. Upon infection, increased turgor pressure at the tip of the appressorium allows it to mechanically penetrate the cuticle and host cell walls (Mendgen and Deising, 1993).

The evidence for enzymatic breakdown of host cell walls is largely cytological. Host cell walls are disrupted at sites slightly removed from the point of *Striga* ingress, suggesting that factors responsible for cell wall dissolution are diffusible (Olivier et al., 1991). Similar cell degradation was not seen when resistant host plants were infected, indicating that cell-wall-degrading enzymes might act differently on the walls of different hosts.

In one of few biochemical studies, the activity of cell wall-degrading enzymes in *Cuscuta reflexa*, a stem parasite in the Convolvulaceae family, was examined (Nagar et al., 1984). The activity of exo-1,4-β-D-glucosidase was about 50 times higher and xylanase was about 100 times higher in haustoria than in surrounding tissue. Pectin pectylhydrolase and polygalacturonase were 2 to 4 times higher in haustoria than in surrounding stem tissue. Polymethylgalacturonase, cellulase, and cellobiase activities were not different between haustoria and nearby tissue.

A further point to consider is that enzymatic degradation of host cells during haustorium entry will result in the release of additional phenolic HIFs. This mechanism would amplify HIFs and signal additional haustoria development when an appropriate host was found. Consistent with this idea, *Triphysaria* sp. haustoria are often clustered on maize roots when plants are grown together for several weeks in pots.

Haustorium Maturation

Developmental changes continue after the haustoria have invaded the host. Among the most obvious are the continued enlargement of haustoria through cortical cell division and expansion and the development of a xylem bridge connecting the host and parasite xylem elements (Fig. 4). Xylem elements are derived from the differentiation of cortical cells within the haustorium, a process that begins at the proximal tip of the haustorium and proceeds toward the parasite root. Host signals are implicated in

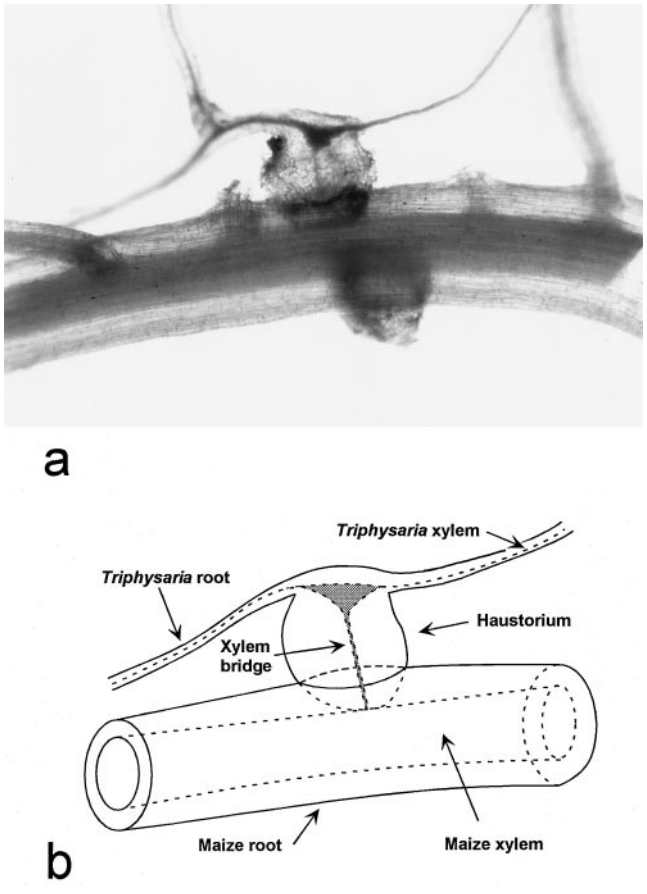

Figure 4. Haustorium attached to a maize root. a, *T. versicolor* plants were grown in pot cultures with maize for about 2 months, after which time the roots were washed clean of soil and fixed in FAA. Roots connected by haustoria were dissected and cleared by autoclaving for 15 min in 75% lactic acid. The xylem bridge is internal to the haustorium. A second haustorium is attached to the underside of the maize root. b, Schematic representation of the cleared haustorium shown in a.

these events because xylem forms only after host contact (Yoder, 1997).

Once xylem connections between the host and parasite are established, the translocation of host materials to the parasite begins. Water, minerals, amino acids, carbohydrates, and other macromolecules are unidirectionally translocated from the host into the parasite. Naturally occurring resistances suggest the role of postinvasion, host-parasite signaling. For example, *S. gesnerioides* penetrates the cortex and establishes a xylem bridge with the resistant cowpea line B301 and yet is unable to develop further (Lane and Bailey, 1992). There are probably additional host functions that contribute to the success and vigor of the parasite at later stages of parasitism; however, these are currently largely undefined.

CONCLUSIONS

How do broad host range parasitic plants such as *Triphysaria* spp. distinguish the presence of host and non-host plants? The answer to this question is not known, but the signaling and detection models described above suggest possible mechanisms.

Because different phenolic molecules act as HIFs, and since several of these are critical to important plant processes such as lignin biosynthesis and pathogen defense, it is unlikely that parasite roots do not make them. In sorghum, HIFs are removed from host cell walls and activated by parasite-specific enzymes. Perhaps specificity is realized by differential enzyme accessibility or susceptibility to host cell walls. Once removed from the host cell wall, many of the phenolic acids must be oxidized to the proper redox potential for induction, the conversion of which could also be a species-specific reaction. Alternatively, parasite plants may make inhibitors that repress their own HIF-releasing enzymes. In this light, it is interesting that some phenolic compounds, including DMBQ, can inactivate cell wall-degrading enzymes (Patil and Dimond, 1967).

Host resistance against plant pathogens is generally considered one of the best protection measures with regard to effectiveness, cost, implementation, and environmental soundness. Although some resistances against parasitic weeds have been reported, the characterization, manipulation, and incorporation of these factors into crop plants has been difficult. An elucidation of the mechanisms that limit self-parasitism might suggest novel strategies for engineering resistance against these devastating pests.

ACKNOWLEDGMENTS

We want to thank D. Philips, R. Wrobel, H. Albrecht, and D. Jamison for stimulating discussions. We also thank N. Donner for supplying Figure 3a.

Received August 20, 1997; accepted October 6, 1997.
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